

SUBLITTORAL ECOLOGY OF KELP BEDS OF THE OPEN COAST AREA NEAR CARMEL, CALIFORNIA

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The intertidal fauna and flora of the Monterey Bay area in central California are well-known, but the immediate subtidal associations, especially on the open coast where *Nereocystis* kelp predominates, are largely unexplored in places exposed to surf action. Free diving with the aqualung now makes possible direct observation of sublittoral zones (Drach, 1958).

METHODS

Diving along the open coast was undertaken in selected locations approximately nine miles south of Carmel, near Granite Creek ($36^{\circ} 26.5' N$. Lat., $121^{\circ} 55.5' W$. Long.), between August, 1959, and September, 1961. This report is based on observations and collections made on 30 dives, amounting to approximately 20 hours underwater. Eleven dives were made during the summer of 1959, nine were made during the summer of 1960, and ten dives were made in alternate months during the fall, winter and spring of the two-year period of observation.

Diving from protected shore areas is possible in the summer during the calm periods associated with most low tides, but during the winter months continuous heavy swells make diving possible only on exceptionally calm days. After each dive, the collected material was identified and all observations recorded. During calm weather visibility may exceed 40 feet, but following rough weather or during phytoplankton blooms, it may be restricted to less than 10 feet. The profusion of forms found in sublittoral zones requires the diver to make many successive dives; only when most of the fauna is recognizable is it possible to note different patterns of distribution and to measure or estimate abundance.

OPEN COASTAL CONDITIONS

The coastal area from the Monterey Peninsula south to Point Sur and further south to San Simeon is characterized by steep granite cliffs (Fig. 1). Relatively deep water is found inshore; beaches are few and are usually limited to small coves. The shoreline is highly irregular. Uneven weathering of the granite has left pinnacles, some of which are submerged or constitute small islands. These small islands and projecting reefs afford protected areas in which the water between the open ocean and the shore may be 30 feet deep.

Upwelling is characteristic of this coastal area, producing cool temperatures, especially in the spring and summer. Monthly temperature readings have been made at Soberanes Point, one mile to the north of Granite Creek, by personnel of

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Hopkins Marine Station. Averages of monthly temperatures taken from 1956 through 1960 show a minimum of 10.8°C . in April and a maximum of 13.4°C . in September. The extremes over this five year period were 8.8°C . in June of 1959 and 14.6°C . in September, 1957. At Mussel Point in Monterey Bay, averages of daily readings for the same period reached a minimum of 12.5°C . in February and a maximum of 15.1°C . in September. These readings are approximately two de-



FIGURE 1. The diving area at Granite Creek, looking north. Inshore walls are steep and the small islands afford protected diving areas. *Nereocystis* kelp, shown at the surface, is anchored in depths of 40 feet.

grees higher than on the outer coast to the south where upwelling is prevalent. Salinities in the Monterey Bay area usually vary between 33.5‰ and 34.0‰ depending on the season and rainfall.

The major kelp along the open coast in the Monterey Bay area at depths of 15 to 60 feet is the bulb kelp, *Nereocystis luetkeana*, which develops best in exposed conditions (Hurd, 1916). The *Nereocystis* beds extend only to a distance of 100 to 200 yards offshore where depth rapidly increases. Large stands of the giant kelp, *Macrocystis pyrifera*, are found in the more sheltered areas of Monterey and Carmel bays and south of Point Sur. Occasional plants occur along the open coast in the Monterey Bay area. The *Macrocystis* beds of southern California usually occur well offshore from beaches and are of greater width.

The stipe of *Nereocystis* may reach a length of 60 feet. Blades are produced only on the terminal float. I found that a typical plant has approximately 72 blades, each of which is three inches wide and up to eight feet in length. The blades of a single plant may have an area up to 70 square feet (on one side), hence a very dense surface canopy is produced where *Nereocystis* is aggregated. The holdfast is relatively small, reaching a diameter of only six inches. The stipes are about three-eighths of an inch in diameter in their basal portions. A cable of 10 to 20 stipes twisted together is usually formed where the plants grow thickly.

Nereocystis is an annual plant. Large quantities of this kelp are cast ashore on beaches during the fall months. The surface canopy is usually lost by late December, although a few plants persist through January. Young plants about a foot

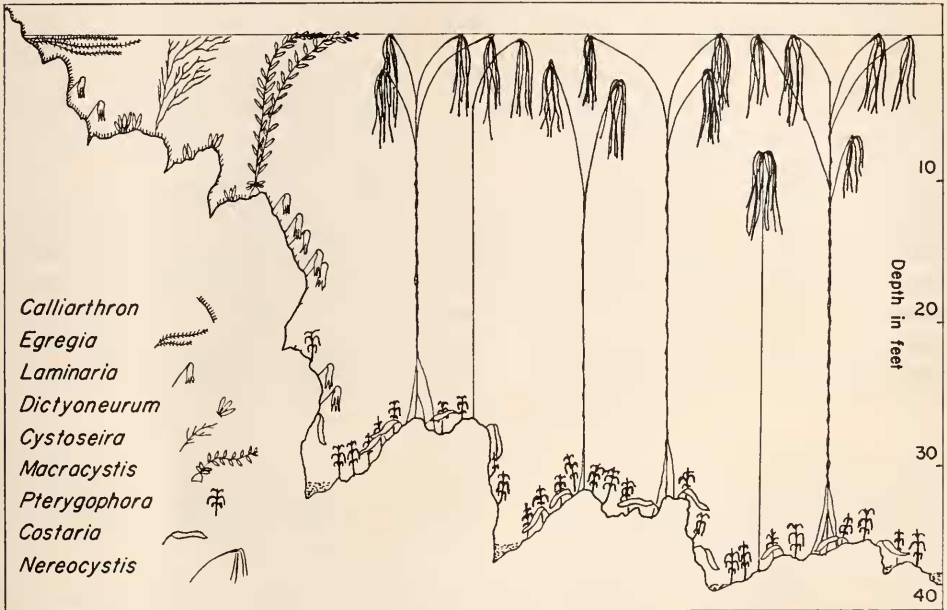


FIGURE 2. Diagrammatic cross-section of the *Nereocystis* kelp bed at Granite Creek, showing zonation of major algae. Depths are in feet below mean low water. The horizontal scale is approximately the same.

in height can be seen in April. In June the surge and tidal currents twist the stipes together before many of them reach the surface. During the late spring, summer, and early fall, the *Nereocystis* canopy exerts a profound shading effect upon its environment.

Intertidal forms are those which characterize the open coast environment described by Ricketts and Calvin (1952). The alga *Postelsia palmaeformis* receives the full force of the surf on rocky points; beds of *Mytilus californianus* are found somewhat lower, and lower still, extensive beds of the purple sea urchin, *Strongylocentrotus purpuratus*, are observed. At about the mean low-tide level in areas protected from the full force of the surf, the ribbon kelp, *Egregia menziesii*, produces a floating canopy extending ten or more feet out. The blades are annual; when

present, this kelp has a significant shading effect upon the immediate subtidal environment.

THE CALLIARTHRON ZONE

The immediate subtidal zone, down to a depth of over ten feet, usually has a dense growth of a branching red coralline alga, *Calliarthron cheilosporioides* (Fig. 2). In southern California and in the more protected areas of central California, such as Monterey Bay, this zone is dominated by the eel grass, *Phyllospadix scouleri*. On level surfaces within this zone, a small kelp, *Dictyonium californicum*, covers large areas. The brown alga *Cystoseira osmundacea* grows thickly at depths to ten feet, producing long floating branches during the summer. Another conspicuous alga of the *Calliarthron* zone is *Desmarestia herbacea*. Numerous red algae characteristic of the low intertidal zone may extend into the subtidal region. The distribution and zonation of these red algae are dependent upon complex factors not considered here, major attention having been directed to the deeper zones. The over-all color of the *Calliarthron* zone is red, due to the alga itself and to *Lithothamnion lamellatum* and *L. californica*, which cover most of the remaining rock surfaces.

Few invertebrates are conspicuous in this zone. Large sessile animals seem unable to compete for space with the dense growth of *Calliarthron*. However, some forms characteristic of the intertidal zone of more protected environments replace *Calliarthron* in crevices. Only a few abundant animals in this zone were considered. The large gill fans of the sabellid worm, *Eudistylia polymorpha*, are conspicuous projecting from crevices. Large leaf-like colonies of the bryozoan *Hippodoplosia insculpta* are also able to gain a foothold among the *Calliarthron*.

THE PTERYGOPHORA ZONE

As the diver descends a typical vertical rock wall, the growth of *Calliarthron* becomes thinner and widely scattered (Fig. 2). Large *Laminaria setchellii* are spaced closer than a foot apart and grow out from the walls at a 45° angle. At a depth of 15 feet a large *Laminaria* may have a stipe five feet in length and a blade area of six square feet. With increasing depth, a profusion of sponges and tunicates appears on the walls. An orange sponge, *Tethya aurantia californica*, several inches in diameter, is conspicuous. On overhung walls, a red alga, *Fryeella gardneri*, produces an iridescent horizontal blade. Colonies of the anemone *Corynactis californica* are plentiful, and the solitary coral *Balanophyllia elegans* is abundant on all rock surfaces. In caves and overhung areas, a dark blue sponge, *Hymen- amphistra cyanocrypta*, covers large areas; a red anemone, *Tealia lofotensis*, is also found here. Sessile animals are most abundant on vertical rock surfaces below 20 feet where competition for space with *Calliarthron* is less extreme. Organisms common on vertical rock walls are listed in Table I.

Large boulders and rock ledges comprise the bottom at depths of 30 to 50 feet. Granitic gravel and shell fragments fill depressions among rocks. Aggregations of the polychaete worm *Diopatra ornata*, with tubes composed of broken shell, are conspicuous at the surface of the gravel. Algal detritus accumulates in thick masses in deep pockets among the bottom reefs.

The bottom rocks support a forest of the laminarian kelp *Pterygophora cali-*

formica. A typical *Pterygophora* plant has the general appearance of a palm tree, with a flattened erect stipe an inch in width and three to five feet long, and about 20 blades having a combined surface area (on one side) of approximately 18 square feet. The stipes are often closer than a foot apart. A rather heavy subsurface canopy is therefore produced, and the diver, swimming above it, will see little of the life beneath this canopy. *Pterygophora* is a perennial plant that lives for

TABLE I

Organisms common on vertical rock surfaces at depths of 20 feet and below

Algae	Polychaeta (cont.)
<i>Laminaria setchellii</i>	<i>Pista elongata</i>
<i>Calliarthron cheilosporioides</i>	Cirripedia
<i>Fryxella gardneri</i>	<i>Tetraclita squamosa elegans</i>
Porifera	Brachyura
<i>Leucoselenia eleanor</i>	<i>Loxorhynchus crispatus</i>
<i>Leuconia heathi</i>	Amphineura
<i>Rhabdodermella nuttingi</i>	<i>Tonicella lineata</i>
<i>Tethya aurantia californica</i>	Gastropoda
<i>Hymenamphistra cyanocrypta</i>	<i>Diodora aspera</i>
Hydrozoa	<i>Calliostoma ligatum</i>
<i>Abietinaria abietina</i>	<i>Ceratostoma foliatum</i>
<i>Aglaophenia latirostris</i>	<i>Ocenebra lurida</i>
Anthozoa	<i>Fusinus luteopictus</i>
<i>Balanophyllia elegans</i>	Pelecypoda
<i>Corynactis californica</i>	<i>Hinnites multirugosus</i>
<i>Anthopleura xanthogrammica</i>	Astroidea
<i>Tealia lofotensis</i>	<i>Henricia leviuscula annectens</i>
Bryozoa	Ascidiacea
<i>Diaperoecia californica</i>	<i>Amaroucium solidum</i>
<i>Hippodiplosia insculpta</i>	<i>Clavelina huntsmani</i>
<i>Phidolopora pacifica</i>	<i>Distaplia occidentalis</i>
Polychaeta	<i>Eudistoma</i> sp.
<i>Eudistylia polymorpha</i>	<i>Polychinum planum</i>
<i>Serpula vermicularis</i>	

several years. The holdfast is nearly as large as that of *Nereocystis*. Unlike the *Nereocystis* stipe, that of *Pterygophora* is woody and slow to decompose. Numbers of detached stipes accumulate in the pockets between rocks.

The streamer kelp *Costaria costata* is found with *Pterygophora*. *Costaria* has an undivided blade over a foot in width and about five feet long that trails along the bottom under the *Pterygophora* canopy. The large blades reach full size in June. Another major alga of the *Pterygophora* zone is *Desmarestia munda*, with branching blades several feet in length. Other common algae include *Dictyota eribosa*, *Plocamium pacificum* and *Polysiphonia paniculata*, each of which grows in conspicuous tufts on tops of boulders not heavily shaded by *Pterygophora*. During the winter and early spring months the absence of *Nereocystis*, *Costaria*, *Desmarestia*, *Cystoseira* and *Egregia* is very noticeable. The diver is no longer in a jungle.

Calliarthron, *Laminaria*, *Dictyoneurum*, and *Pterygophora* remain. The conspicuous smaller algae, such as *Dictyota*, *Plocamium* and *Fryxella*, are likewise reduced during winter months.

One of the more conspicuous invertebrates in the surge channels of the *Pterygophora* zone is the giant green anemone *Anthopleura xanthogrammica*; individuals are often spaced a few feet apart. *Patiria miniata* is the most common starfish and the many-rayed star *Pyncnopodia helianthoides* is often encountered. Mollusks are conspicuous. The large gumboot chiton *Cryptochiton stelleri* is common and *Tonicella lineata* is an abundant chiton seen on all rock surfaces. Aspidobranch gastropods are abundant as species and individuals; an ideal environment is provided for their grazing manner of feeding. *Tegula brunnea* is a common gastropod associated with brown algae; the small *Homalopoma carpenteri* is another abundant gastropod.

TABLE II

Organisms common on level rock surfaces under the Pterygophora canopy

Algae	Anomura (cont.)
<i>Pterygophora californica</i>	<i>Paguristes ulreyi</i>
<i>Costaria costata</i>	
<i>Desmarestia munda</i>	Amphineura
<i>Dictyota cribosea</i>	<i>Cryptochiton stelleri</i>
<i>Plocamium pacificum</i>	
<i>Polysiphonia paniculata</i>	Gastropoda
	<i>Acmaea mitra</i>
Porifera	<i>Acmaea ochracea</i>
<i>Tedania topsenti</i>	<i>Astraea gibberosa</i>
	<i>Homalopoma carpenteri</i>
Bryozoa	<i>Petalonchus montereyensis</i>
<i>Crisia maxima</i>	
	Asteroidea
Sipunculoidea	<i>Patiria miniata</i>
<i>Phascolosoma agassizi</i>	<i>Pyncnopodia helianthoides</i>
Anomura	
<i>Pagurus hemphillii</i>	

The fauna under the *Pterygophora* canopy and on the sides of boulders is not as rich as that found on vertical walls. However, in sites which are well-protected by dense growth of *Pterygophora*, the rock may be encrusted with organisms up to an inch in thickness. These mats contain loose layers of *Lithothamnion*, colonies of the orange sponge *Tedania topsenti*, the feathery bryozoan *Crisia maxima*, small sabellid worms, the sipunculid *Phascolosoma agassizi*, the sessile gastropod *Petalonchus montereyensis*, and numerous other small organisms. On sloping sides of boulders and other areas not protected by a heavy *Pterygophora* canopy, this mat of organisms is not present and is replaced by red corallines such as *Lithothamnion*, *Bossiaella*, and *Corallina*. Organisms common on level rock surfaces are listed in Table II.

Many motile invertebrates and encrusting forms are found under loose rock in the channels between reefs. Some of the common animals found under rock or on the under surfaces of rock are listed in Table III.

Still another association occurs on the stipes and fronds of *Laminaria* and *Pterygophora*, which provide a substrate for gastropods, bryozoans and hydroids. Associated animals are listed in Table IV.

SEA OTTER PREDATION

One large invertebrate that might normally be expected was not found in the areas I studied. Living *Strongylocentrotus franciscanus*, the large sea urchin, was totally absent, although spines and test fragments were present in gravel samples. This appears to be the result of predation by the California sea otter,

TABLE III

Organisms common on under surfaces of loose bottom rocks

Brachyura	<i>Mimulus foliatus</i> <i>Pugettia richii</i> <i>Scyra acutifrons</i>
Amphineura	<i>Ischnochiton radians</i> <i>Lepidozona mertensii</i>
Gastropoda	<i>Haliotis wallalensis</i>
Ophiuroidea	<i>Ophioplocus esmarki</i> <i>Ophiothrix spiculata</i>

Enhydra lutris nereis, maximum populations of which are now found between the Monterey Peninsula and San Simeon, California (Booolootian, 1961). I have occasionally observed them in my diving area. Dr. Richard Booolootian spent eight to ten hours daily during May and June, 1956, observing a herd of 50 animals through a telephoto lens from shore at Rocky Point, two miles to the south of the present area. Fifty sea otters were observed eating 5280 *S. franciscanus*, 301 *Mytilus californianus*, and 380 *Haliotis rufescens* (Booolootian, personal communication). They were found to entirely clean out one urchin bed and move on to another. Their effect upon abalone populations is not fully known. A few

TABLE IV

Animals associated with stipes and fronds of Laminaria and Pterygophora

Hydrozoa	<i>Plumularia lagenifera</i>
Bryozoa	<i>Membranipora membranacea</i>
Gastropoda	<i>Acmaea instabilis</i> <i>Tegula brunnea</i> <i>Tegula montereyi</i>

large *Haliotis* were seen in crevices on the rock walls. The smaller *Haliotis wallalensis* is common under the bottom rocks, although adults of this species may also suffer predation.

The fact that as many as 5280 urchins were taken from a *Nercocystis* community similar to the one I have observed indicates that these urchins would be dominant members of the community in the absence of the otters. Populations of large subtidal urchins are found in many temperate areas of the world and their grazing effects are considerable. Forster (1959) calculated a density of 868 *Echinus esculentus* per acre near Plymouth, England, and determined that their rate of browsing on algae and sessile animals would sweep clear at least one-third

of the rock surface in the course of a year. The effect of *S. franciscanus* has been noted in *Macrocystis* beds in Baja California. Dawson *et al.* (1960, p. 12) reported: "A grounded tanker released crude oil into a small bay on the Baja California coast, killing nearly all of the animals, including the major herbivores such as the sea urchins and abalone. The great increase and luxuriance of plant growth that followed upon the removal of grazing pressure dramatically demonstrated the important part played by these animals in the regulation of the plant association." Grazing effects of *S. franciscanus* have been noted also by McFarland and Prescott (1959), and Limbaugh (1955). Apparently the otters are permitting luxuriant development of the *Nereocystis-Pterygophora* association by their predation upon urchins and, to a lesser extent, abalones. The otters do not range into Monterey Bay. The subtidal rocks in Monterey Bay at Mussel Point at depths of 10 to 20 feet are covered with urchins and abalones spaced only a few feet apart. Although conditions are too calm for good development of *Nereocystis* and *Pterygophora*, all other large algae are heavily grazed upon, and the general appearance of these rocks is barren.

Because of the value of their fur, the sea otters were brought to the brink of extinction by the early part of this century, but under heavy protection they have recently increased in numbers. It is altogether likely that during the period in which they were scarce the urchins were found abundantly in the *Nereocystis-Pterygophora* association and kept this community at a minimum level of development as a result of grazing.

DISCUSSION

In the relatively uniform environment investigated, I have recognized two zones based upon the dominant species of algae in each zone, the immediate subtidal or *Calliarthron* zone, and the deeper *Pterygophora* zone. No well-defined separation exists between the zones I have designated. The usual transition on vertical walls involves a thinning of the *Calliarthron* with increasing depth; replacement is accomplished with large *Laminaria*, *Pterygophora*, and *Costaria*, and increasing numbers of sessile animals. Thickest growth of *Calliarthron* occurs on projecting walls exposed to continual action of surge below the surf areas. Calmer water and some shade are associated with the position of *Pterygophora*. Fully developed plants of the latter alga will not be found shallower than 20 feet.

Kelp zones characteristically extend to depths of 60 to 70 feet; below these depths algae are usually limited to inconspicuous red forms. Forster (1954) examined the transition between the laminarian and sub-laminarian zones near Plymouth, England. Limbaugh and Shepard (1957) described some of the fauna of this deeper zone in the Scripps and La Jolla Submarine Canyons of southern California. The transition could not be observed on the coastal area under consideration because sand replaces the granite boulders at depths of 50 to 60 feet. However, underwater observations at depths of 70 to 100 feet at the head of the Carmel Submarine Canyon, six miles to the north, have confirmed the appearance of many faunal elements including a gorgonian, several anemones, sponges and red algae. A faunal survey of the walls of this canyon is now in progress.

Andrews (1925) studied the fauna associated with *Nereocystis* in Puget Sound and found that the canopy supported only the minute gastropod *Lacuna* and a few

crustaceans. I have noticed no particular species associated with the *Nereocystis* canopy in the present areas. This may be due to the annual life-cycle of the plant and its slimy surface. In contrast, the stipes and fronds of *Macrocystis* support bryozoans, hydroids, gastropods, and many other forms (Limbaugh, 1955). Five top shells are found on *Macrocystis* stands in Carmel Bay: *Tegula brunnea*, *T. montereyi*, *T. pulligo*, *Calliostoma annulatum* and *C. canaliculatum*. The three species of *Tegula* reach comparable sizes on *Laminaria* and *Pterygophora* but the two *Calliostoma* seem to achieve maximum development only on *Macrocystis*.

Holdfasts of kelps likewise create important microhabitats for many small animals. Andrews (1945) examined holdfasts of *Macrocystis* from Carmel and Monterey bays and tabulated seasonal changes in the composition of the holdfast fauna, which included many small species not considered in the present report. He found that the majority of the animals were immature stages of species not restricted to holdfasts, the kelp holdfast providing protection during the early period of growth. He had found (Andrews, 1925) that the fauna of holdfasts of *Nereocystis* in Puget Sound yielded some 40 species of gastropods, polychaetes, brittle stars and amphipods. The *Pterygophora* holdfast is as large as that of *Nereocystis* and probably supports as many animals.

A considerable amount of light is removed by the *Nereocystis* canopy during the summer. Most of the light which penetrates through this canopy is then absorbed by the heavy subsurface canopy of *Pterygophora* and *Costaria*. Measurements taken under the *Pterygophora* canopy with a photoelectric light meter in a glass jar showed a loss of over 95% of the light available immediately below the surface. Loss of this amount of light characterizes kelp forests of temperate coasts. Kitching (1941) found that laminarian kelps at Carsaig Island, Scotland, cut off 99% of the available light at depths of one to six meters, the illumination changing very little over this depth range. Similar light penetration measurements have also been made within southern California *Macrocystis* beds by McFarland and Prescott (1959).

Kelp communities are highly productive. McFarland and Prescott (1959) measured wet standing crop, chlorophyll content, and *in situ* metabolism of a giant kelp community in southern California and found that a *Macrocystis* kelp bed produces yields comparable to other highly productive communities such as coral reefs and marine grass flats. The *Nereocystis-Pterygophora* community probably has a similar productive capacity, judging from the amount of light absorbed.

The *Macrocystis* beds of southern California have become relatively well-known through recent publications (Limbaugh, 1955; Aleem, 1956; McFarland and Prescott, 1959; Dawson, Neushul and Wildman, 1960). The *Nereocystis-Pterygophora* beds differ chiefly in their inshore position and in the annual life-cycle of *Nereocystis*. During the winter they are more comparable to laminarian kelp beds studied in the European north Atlantic (Gislén, 1930; Kitching, Macon and Gilson, 1934; Kitching, 1941; Drach, 1949; Forster, 1958; Kain, 1960). The north Atlantic fauna reported by Forster is similar in many ways to that in the present study. He found a similar rich development of *Corynactis*, sponges, bryozoans, and tunicates. Many genera are represented in both localities. A major difference is the scarcity of gastropods, other than nudibranchs in the sublittoral zones near Plymouth. In the *Nereocystis-Pterygophora* beds they are well represented in

species and individuals. For a comparison of common sublittoral forms on the West Coast, descriptions of areas with faunal listings are given by Limbaugh (1955) and Pequegnat (1961) for southern California, and by Shelford *et al.* (1935) for Puget Sound in Washington.

LIST OF SPECIES

An endeavor has been made in the listings that follow to include all common invertebrates and algae that may be taken on rock walls and level bottoms below 20 feet, down to a depth of 50 feet. Such groups as the small crustaceans, free-living polychaete worms and others have been left out entirely. Mollusks and algae have been treated in greatest detail.

The following have assisted me with identifications: Dr. Isabella Abbott and Dr. George J. Hollenberg (algae), Dr. E. Yale Dawson (coralline algae), Dr. Cadet Hand (hydroids), Dr. John D. Soule (bryozoans), Dr. Cyril Berkeley (tubicolous polychaetes), Mr. Victor Zullo (barnacles), Dr. Rolf Bolin (decapod crustaceans), Dr. A. Myra Keen and Mr. Allyn G. Smith (mollusks), and Dr. Donald P. Abbott (tunicates). Many of the invertebrates mentioned are included in the keys given by Light *et al.* (1957). Ricketts' and Calvin's *Between Pacific Tides* is also a valuable reference for this fauna. Both books contain bibliographies that include the more important systematic papers dealing with Pacific Coast fauna.

Species that are limited to subtidal zones or are rare intertidally in the Monterey area are indicated by an asterisk. Species marked with a double asterisk are rare at depths to 50 feet but are common elsewhere in the Monterey area at depths below 70 feet, according to my underwater observations. Organisms listed as abundant may be collected in large numbers during a single dive. Limited numbers of those listed as common may usually be collected during a dive, while "scarce" species may not always be found during a dive, even after intensive search.

MARINE ALGAE

Chlorophyta

Enteromorpha sp. Scarce on unshaded horizontal surfaces.

Cladophora microcladioides Collins. On vertical rock walls.

Spongomorpha coalita (Rupr.) Collins. On walls not heavily shaded.

Derbesia marina (Lyng.) Solier. The *Halicystis*-phase is common on *Lithothamnion* on vertical walls.

Phaeophyta

Ectocarpus acutus S. & G. Abundant epiphyte on *Desmarestia munda* and *D. herbacea*.

Ectocarpus confervoides var. *pygmaeus* (Aresch.) Kjellm. Epiphytic on floats of *Nereocystis*.

Sphacelaria didichotoma Saund. Recorded on *Pterygophora* holdfasts.

**Dictyota cribosea* S. & G. Common on tops of boulders in early summer.

Desmarestia herbacea (Turn.) Lamour. Common in *Calliarthron* zone in early summer.

- Laminaria setchellii* (Eaton) Silva. (Syn. *L. andersonii*.) Conspicuous on vertical walls throughout the year.
- Costaria costata* (Turn.) Sand. Common with *Pterygophora* during the summer and fall.
- Dictyoncurum californicum* Rupr. Common in *Calliarthron* zone throughout the year.
- Nereocystis luetkeana* (Mert.) P. & R. Holdfasts on tops of boulders during the summer and fall.
- **Macrocystis pyrifera* (L.) C. A. Ag. Scattered plants throughout the year.
- **Pterygophora californica* Rupr. Abundant below 20 feet throughout the year.
- Egregia menziesii* (Turn.) Aresch. Holdfasts at mean low tide and tops of boulders in shallow water during the summer and fall.
- Cystoseira osmundacea* (Menzies) C.A.Ag. Best developed in *Calliarthron* zone during the summer, non-fruiting plants at greater depths.

Rhodophyta

- Pilea californica* Harvey. Scarce under *Pterygophora* canopy.
- Peyssonnelia pacifica* Kylin. Common encrusting *Tegula* shells.
- Lithothamnion californica* Foslie. Covers most rock surfaces free of sessile animals.
- Lithothamnion conchatum* Setch. & Fosl. Epiphytic on *Calliarthron*.
- Lithothamnion lamellatum* Setch. & Fosl. Forms large crustose sheets in *Calliarthron* zone.
- Lithophyllum licheneare* L. R. Mason. Common in *Pterygophora* zone.
- Bossiella californica* (Dene.) Silva. Common under *Pterygophora* canopy.
- Corallina chilensis* Dene. Common on horizontal surfaces under *Pterygophora* canopy.
- Calliarthron cheilosporioides* Manza. Covers the rock surface in the immediate subtidal zone. Scattered plants at greater depths.
- Plocamium pacificum* Kylin. Forms conspicuous tufts on tops of boulders not heavily shaded.
- Faucheia media* Kylin. Scarce on walls at 20 feet.
- **Fryeella gardneri* (Setch.) Kylin. Common on shaded vertical and overhung walls.
- Rhodomenia californica* Kylin. Common on holdfasts and rock surfaces under the *Pterygophora* canopy.
- **Antithamnion defectum* Kylin. Scarce on rock walls.
- Griffithsia pacifica* Kylin. Scarce on rock walls.
- Microcladia coulteri* Harv. An abundant epiphyte on holdfasts of *Pterygophora*.
- Delesseria decipiens* J. G. Ag. Scarce on rock walls at 20 feet.
- Polynœura latissima* (Harv.) Kylin. Small specimens at 20 feet.
- Botryoglossum farlowianum* (J. G. Ag.) De Toni. Scarce under the *Pterygophora* canopy.
- **Dasyopsis densa* G. Sm. Scarce on rock walls.
- Polysiphonia pacifica* var. *delicatula* Holl. Abundant on exposed bottom rocks in April, 1961.
- Polysiphonia paniculata* Mont. (Syn. *P. californica*) In tufts on tops of boulders.
- Pterosiphonia baileyi* (Harv.) Falken. On rock walls.

Pterosiphonia dendroidea (Mont.) Falken. Common on holdfasts and *Lithothamnion*.

**Pterosiphonia gracilis* Kylin. Recorded on the surface of a colonial tunicate.

Herposiphonia rigida Gardn. Common on *Lithothamnion* and holdfasts.

Amplisiphonia pacifica Holl. On *Pterygophora* holdfasts.

PORIFERA

Calcarea

Leucosclenia cleonor Urban. Finely branched grey masses common on rock walls.

**Sycon coronatum* (Ellis and Solander). A small solitary urn-shaped form scarce on rock walls.

Leuconia heathi (Urban). A sharp-spined globular form common in crevices on rock walls.

Rhabdodermella nuttingi Urban. An urn-shaped form common on walls.

Demospongiae

**Tethya aurantia californica* de Laub. A globular orange form abundant in crevices on walls.

***Polymastia pachymastia* de Laub. Large yellow colonies scarce on flat surfaces and walls.

**Prianos problematicus* de Laub. A soft drab-colored amorphous sponge on walls.

**Tecania topsenti* de Laub. A stiff orange form common on walls and flat surfaces under *Pterygophora*.

Hymenamphiastrea cyanocrypta de Laub. An encrusting purple form on heavily shaded walls.

**Gellius edaphius* de Laub. A stiff drab form scarce on walls.

Aplysilla polygraphis de Laub. Large purple encrusting colonies scarce on walls.

COELENTERATA

Hydrozoa

Eudendrium californicum Torrey. Large branching colonies scarce on walls.

Abietinaria abietina (Linnaeus). Large dark-colored plumes common on walls.

Abietinaria greenei (Murray). A thickly growing tufted form common on walls.

Aglao phenia cf. *A. latirostris* Nutting. A plumed form common on walls.

Sertularella sp. A large plumed form common on walls.

Scyphozoa

Halicystus sp. A small sessile jellyfish scarce on rock walls.

Anthozoa

Balanophyllia elegans Verrill. An abundant orange-colored coral on vertical rock surfaces.

***Paracyathus stearnsii* Verrill. A large solitary coral scarce at 40 feet.

- Anthopleura xanthogrammica* (Brandt). The giant green anemone, conspicuous in crevices and deep surge channels.
- Epiactis prolifica* Verrill. A small anemone common on walls.
- Tealia coriacea* (Cuvier). A red anemone common on walls and in crevices.
- Tealia crassicornis* (Müller). A mottled green and red anemone on walls and under *Pterygophora*.
- **Tealia lofotensis* (Danielssen). A large red anemone common on walls.
- ?*Harenactis* sp. A small burrowing anemone common on gravel surfaces.
- Corynactis californica* Carlgren. A small club-tentacled anemone forming colonies on shaded walls.

BRYOZOA

Ctenostomata

- Flustrella corniculata* (Smitt). A large encrusting form common on stems of *Calliarthron*.

Cyclostomata

- **Crisia maxima* Robertson. Grows erect under the *Pterygophora* canopy.
- **Diaperocia californica* (Orbigny). Large branching colonies common on vertical walls.
- **Heteropora alaskensis* (Borg). Small branching colonies scarce on walls.
- **Lichnopora* cf. *L. novae-zelandiae*. Large purple encrustations scarce on walls.

Cheilostomata

- Bugula californica* Robertson. Finely branched colonies scarce on walls.
- Dendrobania longispinosa* (Robertson). An encrusting form often living on shells of *Diodora aspera*.
- Hippodoplasia insculpta* (Hincks). Erect leaf-like colonies abundant in *Calliarthron* zone, less common in deeper water.
- Lyrula hippocrepis* (Hincks). An encrusting form commonly found on shells of *Ceratostoma foliatum*.
- Membranipora membranacea* (Linnaeus). An encrusting form found abundantly on fronds of *Laminaria* and *Pterygophora*.
- Parasmittina collifera* (Robertson). An encrusting form on shells of *Diodora*.
- Phidolopora pacifica* (Robertson). A lace-like erect form common on walls.
- Rynchozoon tumulosum* (Hincks). An encrusting form on shells of *Diodora*.
- Tricellaria praescuta* Osburn. A finely-branched form commonly attached to sponges and algae.

POLYCHAETA

- Dodocaceria concharum* Oersted. An abundant cirratulid which bores in *Lithothamnion*.
- Sabellaria cementarium* Moore. A sabellariid forming tubes attached to undersides of rocks.

Eudistylia polymorpha (Johnson). A large sabellid, abundant in crevices, especially in *Calliarthron* zone.

Serpula vermicularis Linnaeus. Calcareous tubes common in crevices.

**Spirorbis ambilateralis* Pixell. Common on *Diodora* shells and rocks. Previously known only from Vancouver Island.

Spirorbis spirillum (Linnaeus). Abundant on algae and rocks.

Pista elongata Moore. A terebellid producing tubes with sponge-like openings, common in crevices on rock walls.

SIPUNCULOIDEA

Phascolosoma agassizii Keferstein. Common nestling in holdfasts and sponges.

ARTHROPODA

Cirripedia

Balanus crenatus Brugière. A small form found on *Diodora aspera* shells and rocks.

Balanus nobilis Darwin. A large form recorded on *Diodora*.

Balanus tintinabulum (Linnaeus). A reddish form recorded on *Diodora*.

Tetraclita squamosa elegans Darwin. A large form common on rock walls.

Brachyura

Cancer antennarius Stimpson. A large form on gravel bottoms.

Cancer jordani Rathbun. Small specimens scarce on gravel bottoms.

Cancer productus Randall. Juveniles common on gravel.

Lophopanopeus heathii Rathbun. A small form common on gravel.

Lophopanopeus leucomanus (Lockington). Common on gravel.

**Loxorhynchus crispatus* Stimpson. The masking crab; large individuals cling to vertical walls.

Mimulus foliatus Stimpson. A small red form common under rocks and on gravel.

Pugettia producta (Randall). The kelp crab, on walls and large brown algae.

Pugettia richii Dana. A small form in crevices and under rocks.

Scyra acutifrons Dana. A small form common in crevices and under rocks.

Anomura

Cryptolithodes sitchensis Brandt. A scarce rock crab, found clinging to walls.

Haplogaster cavicauda Stimpson. Scarce in crevices and under rocks.

***Phyllolithodes papillosus* Brandt. An ornate rock crab, scarce on rock walls.

Pagurus granosimanus (Stimpson). A small hermit crab on gravel bottoms.

Pagurus hemphillii (Benedict). A hermit crab using *Tegula* shells, common on gravel and rock bottoms.

**Paguristes ulreyi* Schmidt. A large hermit crab using *Astraca* and *Ceratostoma* shells, common on gravel and rock bottoms.

MOLLUSCA

Amphineura

- Tonicella lineata* (Wood). The lined chiton, abundant on all rock surfaces.
Basiliochiton heathii Pilsbry. Uncommon on under surfaces of rocks.
Mopalia sp. Uncommon on bottom rocks.
Mopalia lignosa (Gould). Common on bottom rocks.
Placiphorella velata Dall. In crevices and on under sides of rocks.
Cryptochiton stelleri (Middendorff). The gum boot chiton, common on rock surfaces.
Ischnochiton radians Carpenter. Common on under surfaces of rocks.
Ischnochiton regularis (Carpenter). Scarce on under surfaces of rocks.
Lepidozona mertensii (Middendorff). Common on under surfaces of rocks.
Stenoplax fallax Pilsbry. A red form scarce on under surfaces of rocks.

Gastropoda

- Acmaea instabilis* (Gould). An abundant limpet on *Laminaria* and *Pterygophora* stipes.
Acmaea mitra Eschscholtz. A common white limpet known to feed on *Lithothamnion*.
Acmaea ochracea Dall. Common on and under bottom rocks.
Acmaea pelta Eschscholtz. Abundant in the intertidal zone, a few individuals occur in deeper water.
Acmaea rosacea Carpenter. A small scarce form on rocks.
Acmaea triangularis (Carpenter). A small limpet on *Calliarthron*, rocks and shells.
Haliotis rufescens Swainson. The red abalone, uncommon in protected crevices.
 **Haliotis wallalensis* Stearns. Common on under surfaces of rocks.
Diodora aspera (Eschscholtz). Large specimens common on rock walls.
 **Diodora murina* (Dall). Scarce on under surface of rocks.
Megatebennus bimaculatus (Dall). Scarce on bottom rocks.
 **Calliostoma annulatum* (Humphrey). Juveniles common on rock walls.
Calliostoma canaliculatum Dillwyn. Juveniles on bottom rocks.
Calliostoma ligatum (Gould). Abundant on rock walls.
Calliostoma splendens Carpenter. A small form scarce on bottom rocks.
 **Margarites parcipictus* (Carpenter). A minute form abundant under rocks.
Margarites salmoncus (Carpenter). Scarce on under surfaces of rocks.
Tegula brunnea (Philippi). Juveniles on rock, adults on *Laminaria* and *Pterygophora*.
 **Tegula montereyi* (Kiener). Common on *Macrocystis*, *Pterygophora* and *Laminaria*.
Tegula pulligo (Gmelin). Juveniles on rocks, adults on *Laminaria* and *Pterygophora*.
 **Liotia acuticostata* (Carpenter). Shells found in coarse gravel.
 **Astraea gibberosa* (Dillwyn). A large form on rock surfaces under *Pterygophora*.
Homalopoma carpenteri Pilsbry. An abundant small form on and under rocks.
Tricolia pulloides (Carpenter). A small form in gravel and under rocks.

Tricolia rubrilineata (Strong). A minute form common on and under bottom rocks.

**Balcis thersites* (Carpenter). Scarce under bottom rock.

**Epitonium indianorum* (Carpenter). Scarce in gravel.

Alvania purpurea Dall. Shells common in gravel.

Barleëia oldroydi Bartsch. A minute form, seasonally abundant under rocks and in gravel.

Diala acuta Carpenter. Common in gravel and under bottom rocks.

Petalococonchus montereyensis (Dall). Colonies on upper surfaces of rocks under *Pterygophora*.

**Petalococonchus* sp. A dark colored form found especially in *Diodora* shells.

Serpulorbis sp. Attached to vertical rock surfaces.

Bittium attenuatum Carpenter. Scarce in gravel and under bottom rocks.

Bittium interfossa Carpenter. Shells found in coarse gravel.

Cerithiopsis diegensis Bartsch. Scarce under bottom rocks.

***Seila montereyensis* Bartsch. Scarce under bottom rocks.

Crepidula adunca Sowerby. Common attached to all large gastropod shells.

Crepidula perforans (Valenciennes). On rock or in apertures of shells occupied by *Pagurus*.

Crepidatella lingulata (Gould). Common on surfaces of small rocks and shells.

Hipponix tumens Carpenter. Shells found in gravel.

Lamellaria rhombica Dall. Scarce on bottom rocks and on gravel.

Velutina laevigata (Müller). Scarce on bottom rocks and on gravel.

Tricia californiana Gray. Shells found in coarse gravel.

***Murex carpenteri* (Dall). Scarce on bottom rocks.

Ceratostoma foliatum (Gmelin). A large murex, common on bottom rocks and in crevices on walls.

***Ocenebra beta* (Dall). Scarce on bottom rocks.

Ocenebra interfossa Carpenter. On bottom rocks.

Ocenebra lurida (Middendorf). Common on all rock surfaces.

**Amphissa columbiana* Dall. Under bottom rocks.

Amphissa versicolor Dall. Common on and under bottom rocks.

Mitrella carinata (Hinds). Common on rock surfaces and algae.

Mitrella tuberosa (Carpenter). Under bottom rocks and on gravel.

Nassarius mendicus (Gould). Scarce on bottom rocks.

Fusinus luteopictus (Dall). Common on rock surfaces.

**Fusinus monksae* Dall. Scarce on rock surfaces under *Pterygophora* canopy.

Cypracolina pyriformis (Carpenter). Common under rocks and on gravel.

Mangelia interlirata Stearns. Scarce on bottom rocks.

Turbonilla (Pyrgiscus) sp. Scarce on gravel surfaces.

Turbonilla (Strioturbonilla) sp. Scarce on gravel surfaces.

Williamia vernalis (Dall). A small pulmonate limpet scarce on rock surfaces.

Nudibranchia

Triopha carpenteri (Stearns). Large specimens of this red and white form common on rock walls.

Cadlina marginata MacFarland. A white form common on rock walls.

Anisodoris nobilis (MacFarland). On rock walls.

Dialula sandiegensis (Cooper). Scarce on rock walls.

Glossodoris macfarlandi (Cockerell). Scarce on rock walls. Known range extended north from San Pedro, California.

Dendrodoris fulva MacFarland. A yellow form common on walls and bottom rocks.

Dendronotus sp. Scarce on rock walls.

Aeolidia papillosa (Linnaeus). Scarce on rock walls.

Hermisenda crassicornis (Eschscholtz). Common on rock walls and bottom rocks.

Pelecypoda

***Chlamys hastatus* (Sowerby). A scarce free-swimming scallop.

Hinnites multirugosus (Gale). The rock scallop, cemented to rock walls.

***Lima hemphilli* Hertlein and Strong. A scarce free-swimming form.

Pododesmus cepio (Gray) Small specimens common on shells and rocks.

Mytilus californianus Conrad. Juveniles on upper surfaces of boulders, apparently torn loose from intertidal zone by storms.

**Modiolus fornicatus* (Carpenter). Nestling in gravel and tunicates.

Mytilimeria nuttallii Conrad. Common in cavities surrounded by compound ascidians.

Milneria kelseyi (Dall). Valves scarce in gravel.

Chama pellucida Broderip. A fixed rock clam in crevices and under sides of rocks.

Epilucina californica (Conrad). Scarce in bottom gravel.

Kellia laperosii (Deshayes). Small specimens commonly nestling in holdfasts and crevices.

Gari californica (Conrad). Scarce in bottom sand and gravel.

Schizothaerus nuttallii Conrad. Scarce in sandy areas away from rocks.

Hiatella arctica (Linnaeus). Common nestling in holdfasts and crevices.

Cephalopoda

Octopus appollyon Berry. Small specimens scarce in rock crevices.

ECHINODERMATA

Asteroidea

**Dermasterias imbricata* (Grube). The leather star, scarce on rocks and walls.

**Evasterias troschelii* (Stimpson). Scarce on walls.

Henricia leviuscula (Stimpson). A small form on rock surfaces.

**Henricia leviuscula* var. *annectens* Fisher. A larger form common on rock walls.

Leptasterias acqualis (Stimpson). A common small form on and under rocks.

Patiria miniata (Brandt). The bat star, conspicuous on bottom rocks.

**Pisaster giganteus* (Stimpson). Scarce on rocks and walls.

***Poraniopsis inflata* Fisher. Scarce on rock walls.

**Pyncnopodia helianthoides* (Brandt). The large many-rayed star, common on bottom rocks.

***Stylasterias forreri* (de Loriol). Scarce at depths of 40 feet.

Ophiuroidea

- Amphiodia occidentalis* (Lyman). Buried in bottom sand and gravel.
 **Amphipholis pugetana* (Lyman). Common on bottom sand and gravel.
Ophioplocus esmarki Lyman. A large form common in crevices and under rocks.
Ophiopholis aculeata forma *kennertlyi* (Lyman). Scarce in gravel.
 **Ophiopteris papillosa* (Lyman). A large form scarce in crevices.
Ophiothrix spiculata LeConte. Abundant in crevices and under rocks.

Echinoidea

- Strongylocentrotus purpuratus* (Stimpson). The small purple urchin; forms extensive beds in the low intertidal zone; small green juveniles common in deeper water.
Strongylocentrotus franciscanus (Agassiz). The large purple urchin, living juveniles scarce; test fragments of adults only.

Holothuroidea

- Eupentacta quinquecemia* (Selenka). A white form scarce on rock walls.
 ***Psolus chitonoides* Clark. A flat-sided red form scarce on walls.
 ***Cucumaria miniata* Brandt. A large drab-colored form scarce in crevices.
 **Cucumaria piperata* (Stimpson). A small spotted form uncommon in crevices.

ASCIDIACEA

Aplousobranchia

- Amaroucium solidum* Ritter and Forsyth. Large red colonies common on walls.
Clavelina huntsmani Van Name. A pink form common on walls.
Cystodytes sp. A common translucent form on walls.
Didemnum carnulentum Ritter and Forsyth. Small white colonies common on walls.
Distaplia occidentalis Bancroft. A variable-colored pedunculate form common on walls.
Distaplia sp. A pale pink form uncommon on overhung surfaces.
Eudistoma psammion Ritter and Forsyth. A dark-brown form common on walls.
Eudistoma sp. An abundant grey form on walls.
Polyclinum planum (Ritter and Forsyth). Large pedunculate colonies common on walls.
Pycnoclavella stanleyi Berrill and Abbott. A small orange form common on walls.
Trididemnum opacum (Ritter). Large white colonies encrusting walls and under surfaces of rocks.

Phlebobranchia

- Chelysoma productum* Stimpson. Scarce on walls and under surfaces of rocks.
Perophora annectens Ritter. A small green form common on walls and holdfasts.

Stolidobranchia

- **Boltenia villosa* (Stimpson). A spiny solitary form common in crevices on walls.
- **Cnemidocarpa finmarkiensis* (Kiaer). A smooth pink form, scarce on under-surfaces of bottom rocks.
- **Pyura haustor* (Stimpson). A large wrinkled solitary form, common in crevices.
- Metandrocarpa taylori* Huntsman. A small red form common on walls.
- **Styela gibbsii* (Stimpson). Common in crevices and on sides of rocks.
- Styela montereyensis* (Dall). A stalked form scarce on walls.

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SUMMARY

1. Aqualung dives along the open coast south of Carmel, California, have been made over a period of two years.

2. The predominant kelp on the open coast in the Monterey area is *Nereocystis luetkeana*; the giant kelp *Macrocystis pyrifera* is scarce. *Nereocystis* is an annual plant producing a heavy subsurface canopy in the summer months.

3. Inshore water is deep; the granite walls drop to a depth of 10 to 30 feet. A dense growth of the branching red coralline alga *Calliarthron cheilosporioides* carpets the immediate subtidal rocks to a depth of 10 feet, to the exclusion of most sessile animals.

4. Below this zone large *Laminaria setchellii* replace *Calliarthron* and a profusion of sponges and tunicates occurs on the walls. The rock bottom at depths of 20 to 50 feet supports a forest of the perennial kelp *Pterygophora californica* which produces a subsurface canopy.

5. A typical *Nereocystis* plant presents 70 square feet and a *Pterygophora* plant 18 square feet of light absorbing area (on one side).

6. The most abundant large invertebrates are an anemone, *Anthopleura xanthogrammica*, the gum boot chiton, *Cryptochiton stelleri*, and the bat star, *Patiria miniata*.

7. *Laminaria* and *Pterygophora* stipes and holdfasts provide important microhabitats for many small animals.

8. Large urchins, *Strongylocentrotus franciscanus*, are absent. California sea otters are known to prey heavily upon this species, probably accounting for its local extinction. I suspect that the absence of this urchin allows the luxuriance of algae and sessile fauna that is observed.

9. A total of 248 species from the sublittoral zone in this locality is listed.

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